THE PLACE OF FERNS AND SEED PLANTS IN CLASSIFICATION.

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THE classification of vascular plants has been based largely on the mature structure of seedling and adult stages of the plant. As knowledge of that structure increased in scope and detail, so the general plan of the classification has been altered. Recently, attention has been given to the structure and activity of apical meristems; and information is now becoming available for use in solving problems of classification. In considering the place of ferns and seed plants in classification, this paper does not discuss the relative merits of the theories of the leaf put forward by Bower (1935) and Zimmermann (1930), nor the grouping of ferns and seed plants with bryophytes as the Embryophyta by Campbell (1940). But, assuming the widely used current concept of a sub-kingdom Tracheophyta (vascular plants) with four divisions—Psilopsida, Lycopsida, Sphenopsida and Pteropsida—it inquires into the status of the fourth division—Pteropsida—and proposes the substitution of two divisions for it: Filicopsida and Spermatopsida.

A great step forward from the older division of vascular plants into Pteridophyta and Spermatophyta was made, about 1900, when Jeffrey (1899a, 1899b, 1908 and 1917) distinguished between the Lycopsida (microphyllous and cladosiphonic, without leaf gaps in the vascular cylinder—cf. 1899a, pp. 186–7) and the Pteropsida (macrophyllous and phyllosiphonic, with leaf gaps in the vascular cylinder—1903, p. 143). By this he removed the ferns from the previous close association with club mosses and horsetails, and associated them with the seed plants in the Pteropsida. (He included *Psilotum* and *Tmesipteris* in the "Lycopodiales" among the club mosses—1903, p. 134). This change was based on the comparison of general body structure, particularly in regard to vascular anatomy. Scott (1909) quickly recognised that from the "Lycopsida" (vascular plants other than Pteropsida) there should be separated off the horsetails as the Sphenopsida (pp. 616–7) but with the inclusion of *Psilotum* and *Tmesipteris* in this new group.

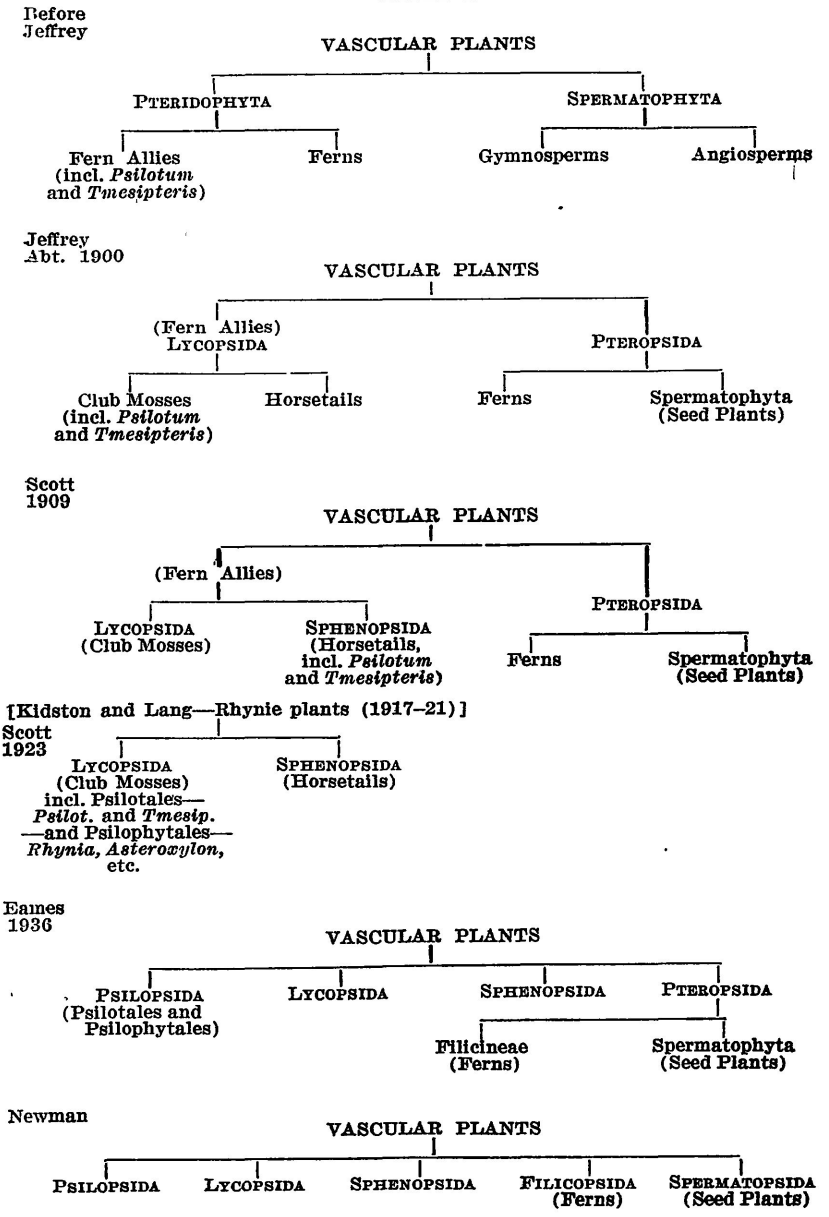
The vascular plants of the Devonian chert at Rhynie, described by Kidston and Lang (1917–1921) were at first included in a separate group called Psilophytales (see Scott, 1920 and 1923). Subsequently, *Psilotum* and *Tmesipteris*, as the Psilotales, were separated from the remaining "Lycopsida" (in which Scott—1923, p. 396—had replaced them) and associated with the Psilophytales to form the new group, the Psilopsida (see Eames, 1936, pp. 114, 330, 405). Thus, between 1930 and 1940, there was clearly set out the classification of the sub-kingdom Tracheophyta* into the four divisions: Psilopsida, Lycopsida, Sphenopsida and Pteropsida (see Eames, 1936, pp. 401–3). Hereby the original heterogeneous division "Lycopsida" is replaced by three more clearly defined divisions, with the original Pteropsida remaining unchanged. Though using different terms for them, and according them different taxonomic ranks, many authors have accepted the validity of these four groups (see Darrah—1939, p. 153—for discussion). It should be recognised, however, that the Psilopsida is a group with indefinite boundaries. Its Silurian and Devonian members represented a level of organisation of the plant body in a world-wide vascular flora, rather than a coherent taxonomic group, and already showed foreshadowings of structural specialisation leading towards the body forms later achieved in the other three divisions. These changes in classification, together with the proposal in this paper, are summarised in Table 1.

In the division Pteropsida, then, the ferns and seed plants (Filicineae and Spermatophyta of Eames—1936, pp. 401–5—or Filicales and Spermophyta of Scott—1909, p. 616) are held together by recognition of their leaves as macrophyllous, by their possession of leaf gaps in the vascular cylinder and by the abaxial, foliar position of their sporangia (Jeffrey, 1908 and 1917). Botanists must always have felt some discomfort about this association, because of the great contrast between dispersal as spores and dispersal as seeds. Perhaps we have

* On the validity of the name Tracheophyta, which does not affect the argument of the present paper, see Just, 1945, pp. 306–7.

salved our consciences by thinking that the distinction was at bottom one of function rather than one of form. But differences not so easily passed off are that, in the ferns, sporangia arise from the epidermal layer only, whereas in seed plants the epidermal layer gives rise only to the epidermis of the "sporangium"; and that, in the ferns, branching is not regularly associated with the position of the leaves, whereas, in seed plants it is axillary to the leaf. Recognition of this distinction leads to a consideration of the initiation of branches and leaves on the plant and of the structure and function of the apical meristem.

TABLE I.



When branching of the stem is considered in relation to apical growth, a sharp cleavage appears between ferns and seed plants. *In the ferns*, primary branching associated with apical growth is infrequent and, when it occurs, is prominently dichotomous and terminal in ontogenetic origin. *In the seed plants*, primary branching associated with apical growth is frequent, axillary, and lateral in ontogenetic origin. The original situations may be masked by subsequent variation in rate and extent of growth (see also Bower, 1923, ch. IV).

In the histological organisation of the growing apex of the vegetative shoot another sharp cleavage appears between ferns and seed plants. *In the ferns*, the tissues of any one axis and its laterals can be traced back to *one* apical cell in the leptosporangiate members and to *one to four* apical cells in the eusporangiate members; the apical cells are superficial, and there is no differentiation within the initiating group (if more than one cell); the superficial layer and all inner layers have a common source in this originating cell or cells (see Bower, 1923, p. 9). *In the seed plants*, the tissues of any one axis and its laterals cannot be traced back to "apical cells," but are derived from a meristem of *many* cells; the meristem is several layers in depth, is variable in depth and is internally differentiated (Priestley and Swingle, 1929; Schüepp, 1926; Louis, 1935; Schmidt, 1924; Priestley, 1928 and 1929); the superficial layer of the shoot originates from cells distinct from those originating the inner layers. This difference in apical organisation is to be observed clearly by comparing Figs. 1 and 2, which are generalised diagrams of the stem apex of fern and seed plant, respectively.

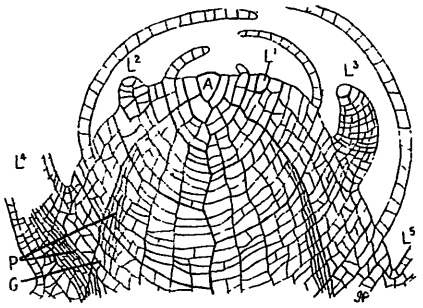


FIG. 1.—The Fern.

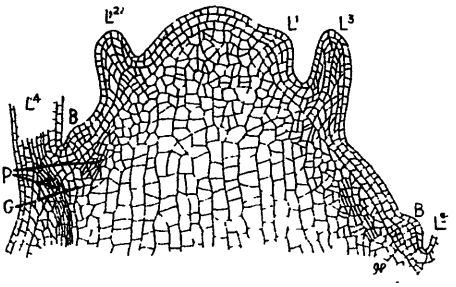


FIG. 2.—The Seed Plant.

Explanation of Text Figures.

TEXT FIGURES 1 and 2.—Generalised diagrams of the cellular structure as seen in longitudinal section of the apices of the vegetative shoot of fern and seed plant respectively.

Cell initiation: In the fern, Fig. 1, is by the apical cell (A), the derivatives of whose initial segments can be followed for some distance back; in the seed plant, Fig. 2, is by an internally differentiated zone of cells lying approximately between L^1 and L^2.

Leaf initiation: In each figure L^1 shows the initiation of the youngest leaf primordium; L^2 and L^3 are young primordia without procambial development yet; L^4 and L^5 are the bases of young leaves, with developing procambium (P) and the leaf gap (G) shown in the case of L^4.

Primary branching: In the seed plant alone, Fig. 2, primordia of branches (B) are shown in the axils of L^4 and L^5; in the case of the fern, Fig. 1, branching, if shown, would be a dichotomy involving the institution of two equal apical cells.

Ramenta are present on the fern apex, but not on the seed plant apex, in these figures.

Finally, in the ontogenetic origin of leaves there is a sharp cleavage between ferns and seed plants, the difference being probably an expression of the different organisation of the shoot apices. It is made clear in Figs. 1 and 2. *In the ferns*, the leaf arises from superficial cells alone (one only in leptosporangiate ferns) from which, after several irregular divisions, the apical cell (or cells) of the leaf is organised. *In the seed plants*, the leaf arises from a zone of cells several layers in depth, of which the outermost layer (epidermis) gives rise only to the epidermis of the leaf, one or more inner layers of the zone giving rise to the body of the leaf which, if it grows by an apical meristem, has that meristem differentiated as in the stem apex (Priestley and Swingle, 1929; Schüepp, 1926;

Louis, 1935; Schmidt, 1924; Priestley, 1928 and 1929). [For discussion of leaf initiation see Newman (1936, pp. 68–72) and Foster (1936 and 1939)].

The ontogenetic origin of the fern leaf (a macrophyll or megaphyll) from one or a very few superficial cells may be regarded as in harmony with Bower's concept of it as phylogenetically derived from a dichopodial branch system in which one half of a dichotomy has been modified and overtopped (1935, ch. XXVII and XXX). The leaf-initiating cells show the histological features we could expect to find when the delayed half of a dichotomising apex of fern type finally comes into activity. But in the seed plants, if the leaf is to be regarded as a "macrophyll" (or "megaphyll") of phylogenetic origin similar to that of the fern leaf, then it would appear that the apex of the seed-plant ancestral dichopodial system was different in organisation from that of the fern ancestral dichopodial system. To this difference there is added in the seed plants the presence of axillary branching.

In view of these differences in organisation of the plant body, both structurally and meristematically, and in the phylogenetic implications of these differences, it is reasonable to remove the ferns and seed-plants from close association in the one division, Pteropsida, and to erect them into two divisions of the Tracheophyta. I propose, therefore, that five divisions of the Sub-kingdom Tracheophyta be recognised, three of them microphyllous and *without* leaf gaps in the vascular cylinder: Psilopsida, Lycopsida and Sphenopsida; and two of them macrophyllous and *with* leaf gaps in the vascular cylinder. The terms "microphyllous" and "macrophyllous" should be taken as indicating, in either case, a similar manner of phylogenetic origin of foliar organs and not necessarily a close phylogenetic relationship.

For the two divisions replacing the "Pteropsida," I propose the names FILICOPSIDA *and* SPERMATOPSIDA: *the name Filicopsida to be applied to the ferns, formerly the Filicineae (see Eames, 1936, p. 401) or the Filicales (see Scott, 1909, p. 616; and Bower, 1923, p. 54); the name Spermatopsida to be applied to the seed plants (Gymnospermae and Angiospermae), formerly the Spermatophyta (see Rendle, 1930, p. 32, and Eames, 1936, p. 401) or Spermophyta (see Scott, 1909, p. 616).*

It is desirable that the rules of nomenclature should be followed in the naming of new groups, of whatever taxonomic rank. But at present there is very little application of the rules above the levels of species, genus, family and order, and so there is little, if any, precedent of application at the level of divisions (Just, 1945). In the present case there is difficulty in applying the International Rules of Botanical Nomenclature, for there is no clear hierarchy of type names leading back for the Pteropsida of Jeffrey (1899b, 1903, 1908, 1917). The splitting of the Lycopsida of Jeffrey (1899a, 1899b, 1908, 1917) into the present three divisions has still left a possible hierarchy of type names in each case:

Psilopsida	— Psilotales	— Psilotaceae	— *Psilotum*
Lycopsida	— Lycopodiales	— Lycopodiaceae	— *Lycopodium*
Sphenopsida	— Sphenophyllales	— Sphenophyllaceae	*Sphenophyllum*

But retention of the name Pteropsida for the ferns after excluding the seed plants would give the possible hierarchy:

Pteropsida — Filicales — Polypodiaceae — *Pteridium*

On the other hand, the proposed name Filicopsida for the ferns would give no less an approximation to the rules in the possible hierarchy:

Filicopsida — Filicales — Polypodiaceae — *Pteridium*

A search for a type species among Jeffrey's papers (1899a, 1899b, 1903, 1908) reveals equal claims for *Pteris aquilina* (now *Pteridium aquilinum*) and a number of species from several families of Angiosperms and Gymnosperms as the type for the "Pteropsida." There can therefore be no rigid obligation to retain the name Pteropsida for the division containing any one of the possible type species. In dropping the name Pteropsida, we would avoid historical confusion with the original use of the term, on the one hand, and with the former Pteridophyta, on the other hand. The new name Filicopsida would have the advantage of maintaining historical continuity with earlier terms for the ferns. The new name Spermatopsida would maintain historical continuity with earlier terms for the seed plants, and, at the same time would indicate the new taxonomic status of the group. Moreover, if so desired at a later date, the two classes of the Spermatopsida could be erected into divisions, conveniently named Gymnospermatopsida and Angiospermatopsida.

The two new divisions, Filicopsida and Spermatopsida, proposed in this paper, may be characterised by the following nine features:

FILICOPSIDA.	SPERMATOPSIDA.
1. Ultimately free-living, vascular zygotic* plants (sporophytes).	
2. Leaves as modified major branch systems (macrophyllous).	
3. Leaf gaps in the vascular cylinder (when siphonostelic).	
4. Sporangia foliar and abaxial.	
5. One superficial apical cell or 1–4 uniform superficial apical cells as initiators of structure.	5. Differentiated, massive meristem, several layers deep, as initiator of structure.
6. Primary branching at the apex of the shoot infrequent, prominently dichotomous† and terminal.	6. Primary branching at the apex of the shoot frequent, lateral, and axillary to the leaves.
7. Leaves arise from one or a very few superficial cells and develop superficial apical cells.	7. Leaves arise by combined activity of a zone of cells several layers deep, and develop a meristem, which, if apical, is massive and differentiated.
8. Sporangia of only epidermal origin.	8. Sporangia of essentially hypodermal origin.
9. Dispersed as spores.	9. Dispersed as seeds.

The first feature is held in common with all other Tracheophyta. The second, third and fourth features, held in common, formerly united the two proposed divisions as the Pteropsida. It is on account of the remaining five differentiating features that it is proposed to create the new divisions Filicopsida and Spermatopsida to replace the former division Pteropsida.

The foregoing matter covers a very wide field; and finality of judgment on the proposition would require the application to it of specialist knowledge in several branches of botany. In this paper there are a number of general statements that require confirmation or variation through further research, though they are generally current in botanical thought. Prominent in this research should be experimental studies on fundamental concepts: work such as that done by Wardlaw (1944a, 1944b, 1945) on the relations between leaf primordia, leaf gaps, bud development and apical meristems in ferns; and by Ball (1946) with tissue culture of shoot apices of Angiosperms. Indeed, the concept of the leaf gap itself comes up for review, at least in connection with Angiosperms, as the result of the work of Dormer (1946), whose exposition of the "acacian vascular system" shows "leaf gaps" of a type not directly referable to the leaf gaps apparently envisaged by Jeffrey (1899a, 1899b, 1903, 1908, 1917) in specifying the Pteropsida. It is, however, significant that this "acacian vascular system" appears directly comparable with the primary vascular system of *Calymmatotheca hoeninghausi (Lyginopteris oldhamia)* as expounded by Scott (1923, pp. 28–32, especially Fig. 17), an exposition difficult to reconcile with the conception of the leaf gap as put forward by Bower (1923, 1935). In fact, further investigations may remove the leaf gap from among the features common to the two divisions and place it among the differentiating features. Nevertheless, I believe that the general picture presented above is substantially sound enough, for the present, to warrant the proposed advance in the classification of vascular plants.

The progress of botanical knowledge has now attained to a range and wealth of detail such that it is not only possible, but greatly desirable, to regularise the specification of the higher groups in the classification of plants and to establish valid names for them. As one whose recent years have been spent solely on teaching, and teaching over the whole range of Botany, I have had this

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* i.e., with the prominent soma developed between syngamy (fertilization) and meiosis (reduction).

† Cases of departure from this are held within the division by other features.

problem strongly forced on my attention. The proposal made in this paper is offered as a contribution towards the solution of the problem, and in the hope that it will stimulate thought and evoke criticism. Left haphazardly to the interest of isolated workers, the conclusion of the matter will tarry. Agreed specifications and nomenclatural validity of the major groups of the Plant Kingdom will be most quickly established by one or more workers being set aside at an institution which, by its location and size, can provide adequate facilities of library, laboratory and liaison.

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P.S.—Recent work by Wardlaw (see above) would modify the figure given here for the fern apex, by a small-celled tissue (meristematic) stretching across from the ends of the procambia to form a concave zone below the apical cell. This may not be universal among the ferns.—I. V. N., June, 1948.

EVOLUTION OF THE ALIEN FLORA OF NEW ZEALAND.

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THE alien flora may be defined as that group of non-native plants (in this paper confined to Dicotyledones, Monocotyledones, Gymnospermae and Pteridophyta) that exist in the non-cultivated state in New Zealand.

The documented history of the evolution of the alien flora of New Zealand commences in 1786 with the publication of Forster's *Florulae Insularum Australium Prodromus*, wherein is recorded the first alien species—canary grass (*Phalaris canariensis*), giving a definite evolutionary period of 160 years. It is possible that the initial stage of the evolution commenced about 1150 A.D. with the arrival of Toi, the first of the Maori voyagers, and continued through the pre-pakeha period to 1769, the arrival time of Cook's first expedition. The taro, paper mulberry, etc., were intentionally introduced during that period, and it seems feasible to suggest that such cosmopolitan species as *Oxalis corniculata*, *Calystegia sepium*, *Solanum nigrum*, and *Sonchus* sp. came in as "stowaways," perhaps in the soil about the roots of the useful plants; some of these species were collected by Banks and Solander, and had every appearance of aboriginal species.

Two essential factors for the development of an alien flora are that there exists the necessary commercial intercourse between the particular region under consideration and other countries by which seeds can be introduced, and that a suitable environment is present for the establishment of the species so introduced. In the case of New Zealand, contact with overseas was initiated by the English and French expeditions which came at the beginning of the pakeha period. and was continued by the increasing advent of whalers, sealers and timber seekers who established bases in New Zealand. Samuel Marsden introduced farm livestock and initiated general agricultural activities in 1814, and was followed by other missionaries and the establishment of more missionary stations, and by 1840 considerable overseas trade was taking place, and the Bay of Islands had become a commercial centre.

After 1840, active colonization was the order of the day, and the area under settlement was increasing rapidly every year; large tracts of tussock grassland were taken up for pastoral purposes and were being sown with English grasses; land was being felled and/or burned out of forest and seed was sown on the ash. This widespread sowing of imported grass-seed mixtures with high content of extraneous seeds up to the time when local supplies of relatively high purity were available was responsible for the introduction of a large number of aliens, and for their widespread dispersal. The imported seed of many agricultural crops accounted for more introductions and has even been operative in recent years.